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**Human infants' ability to perceive touch in external space develops
postnatally**

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Arriving in the outside world, the newborn infant has to determine how the tactile stimulation experienced *in utero* relates to the spatial environment newly offered up by vision, hearing and olfaction. We investigated this developmental process by tracing the origins of the influence of external spatial representation on young infants' orienting responses to tactile stimuli. When adults cross their hands or feet they typically make more tactile localization errors than otherwise, and this has been attributed to the conflicts between skin-based and external frames of reference and/or the usual and current locations of touches in external space [1,2]. Here, we report that a group of 6-month-olds, like adults, showed a tactile localisation deficit with their feet crossed, indicating external spatial coding of touch. In striking contrast, 4-month-olds outperformed the older infants showing no crossed-feet deficit. Thus, in the first months of life, infants perceive touches solipsistically, and only come to locate them in the external world after significant post-natal experience.

A widely accepted account of perceptual development posits that putatively amodal aspects of the environment including spatial location are readily available to perception from birth [3,4]. Until now, research on tactile spatial perception with young human infants has, consistent with that view, shown that even in early infancy manual responses to touch are influenced by the posture of the limbs in external (visual) space [5]. Less consistent, however, is research showing that congenitally blind adults, even if sight has been restored around the second birthday [6], show no crossed hands deficit in contrast with late blind and sighted participants [7]. This suggests a sensitive period in early life in which visual experience is required for the typical development of external spatial representations of touch.

We investigated whether the external spatial coding of touch may emerge in post-natal development before the youngest age at which a crossed-hands effect has

been observed (6 months [5]). Reasoning that the effects of visual experience on tactile spatial representation are likely mediated by the onset of successful reaching at around five months of age, we predicted that 6-month-olds would show a crossing effect whereas 4-month-olds would not. Due to difficulties inherent in crossing young infants' arms, we examined responses to tactile stimuli on the feet across both crossed- and uncrossed-feet postures (Fig. 1A). Crossed-feet effects have been observed in adults [1], and it is known that infants gain visual-tactile experience by reaching with their feet as well as their hands [8]. We measured tactile localisation by observing across several trials whether the first foot movement following a vibrotactile stimulus was made with the stimulated or unstimulated foot [5].

--Insert Figure 1 about here--

We computed the proportion of total foot orienting responses which infants made with the foot receiving the tactile stimulus (i.e., correct unilateral responses / total number of responses) (Fig. 1B). A 2 (Posture: Uncrossed / Crossed) x 2 (Age: 4-month-olds / 6-month-olds) mixed analysis of variance (ANOVA) of this score revealed a Posture x Age interaction that qualified main effects of Age and Posture. Four post-hoc comparisons (see Fig. 1), demonstrated that: i) 6-month-olds showed reliably better localization in the uncrossed than in the crossed posture condition, whereas the 4-month-olds performed equivalently across conditions, and ii) there was equivalent performance between the age groups in the uncrossed posture, but the 4-month-olds significantly outperformed the 6-month-olds in the crossed posture.

The mean latencies of the infants' foot responses (Fig. S1) were entered into a mixed 2 (Posture: Uncrossed / Crossed) x 2 (Age: 4-month-olds / 6-month-olds) ANOVA, which revealed only a main effect of Age (see Fig. S1), in which the 4-month-olds responded more rapidly than the 6-month-olds. Given the 4-month-olds'

faster responding, we considered whether their orienting responses might be more reflexive than the 6-month-olds by comparing the prevalence of responses which comprised gross withdrawal movements or more fine (exploratory) movements (all responses were coded as one or the other; see Supplemental Experimental Procedures). Gross withdrawal responses contributed statistically equivalent proportions across both 4- and 6-month-olds ($M=.12$, $SD=.11$ and $M=.12$, $SD=.09$ respectively), $t(28)=.01$, $p=.99$, $d=.0$.

Thus, the influence of external spatial coordinates on tactile localization emerges between 4 and 6 months of age during human infancy. At 6 months, infants were less accurate in their orienting responses to vibrotactile stimuli on the feet when their limbs were in unusual spatial positions. In contrast, the 4-month-olds showed no influence of the location of a touch in the environment on tactile orienting accuracy. They matched the best performance of the 6-month-olds across both postures, outperforming the older infants in the crossed-feet posture. These striking findings indicate that early in the first year human infants exist in a state of tactile solipsism perceiving touches only in relation to anatomically defined coordinates. An early inability to appreciate the spatial interface between the body and the outside world places strong constraints on early knowledge of the physical environment, demonstrating that early spatial representations are not amodal [3,4].

By 6 months of age, an appreciation of the location of touches in external space leads to poorer performance when the limbs are crossed. Furthermore, the 6-month-olds were also slower to respond to touches on their feet whatever the posture of their legs. This decline in response speed is consistent with an account of representational change in which more processing time is needed to locate a tactile stimulus on the body and in external space than on the body alone [9], but is

inconsistent with accounts appealing to developmental increases in either automaticity of external spatial coding, or prior expectations concerning the external location of the limbs (see Supplemental Information). These declines in accuracy and speed are only temporary set-backs though. Children and adults continue to show crossed-limb deficits in some contexts [1,2,8], but in the simple task of orienting manually to the location of an isolated touch, 10-month-olds are able to adapt to changes in the posture of the limbs, responding at similar response latencies to the 4-month-olds [5,10].

Early in infancy touch is perceived purely with respect to the body. After more than 4 months of experience outside the womb, visual experience [6,7] puts infants in touch with the outside world.

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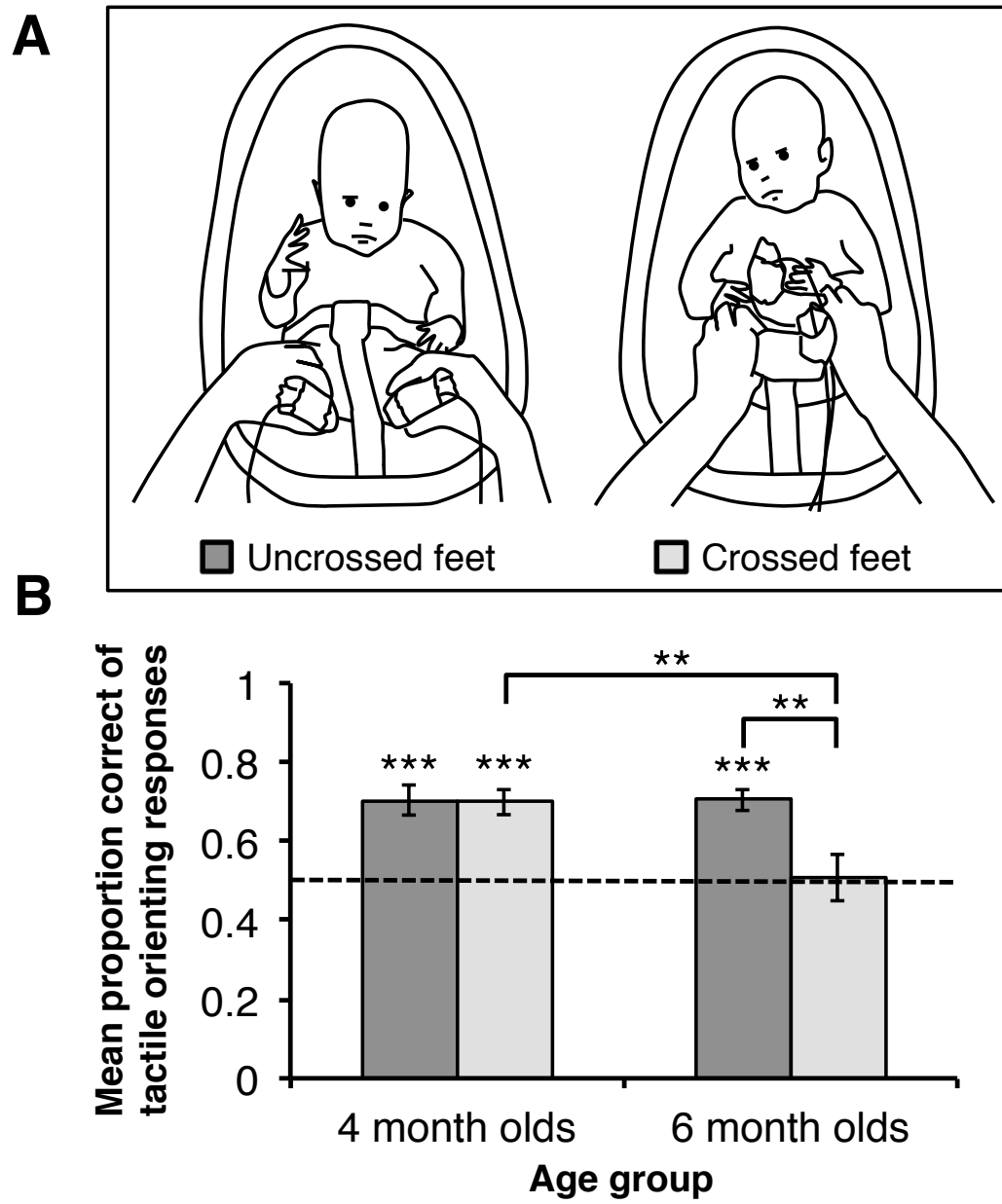
SUPPLEMENTAL INFORMATION

Supplemental Information includes experimental procedures, one figure and one table, and can be found with this article online at *bxs. Supplemental Information: Document S1. Experimental Procedures, One Figure and One Table.

FIGURE CAPTIONS

Figure 1: Probing infants spatial representations of touch by crossing the legs. (A) An infant participant in the uncrossed and crossed feet postures, viewed from above. The tactors, which were attached to the infants' feet using a cohesive bandage, were controlled remotely. The experimenter held the infant's feet in the assigned posture during tactile stimulation. Panel A functions as the legend to Panel B. (B) Mean proportion of correct first unilateral foot movements to vibrotactile stimuli. Error bars indicate the standard error of the mean. An ANOVA revealed main effects of Posture, $F(1,28)=7.0$, $p=.013$, $\eta_p^2=.2$ (uncrossed: $M=.7$, $SD=.13$; crossed: $M=.62$, $SD=.19$), and Age, $F(1,28)=4.3$, $p=.048$, $\eta_p^2=.13$ (4-month-olds: $M=.70$, $SD=.12$; 6-month-olds: $M=.61$, $SD=.12$), and a Posture x Age interaction, $F(1,28)=4.4$, $p=.046$, $\eta_p^2=.14$. The post-hoc comparisons described in the main text (α was $p=.0125$) revealed that the 6-month-olds were more accurate at localising in the uncrossed than in the crossed condition, $t(12)=3.3$, $p=.007$, $d_z=1.21$, whereas the 4-month-olds performed equivalently across conditions, $t(16)=.4$, $p=.690$, $d_z=.12$. There was no difference between ages with uncrossed feet, $t(28)=.4$, $p=.730$, $d=.07$. However, the 4-month-olds outperformed the 6-month-olds with crossed feet, $t(28)=3.0$, $p=.006$, $d=1.08$. One-sample t-tests (two-tailed) revealed that the 4-month-olds performed reliably above chance (0.5) in with both uncrossed, $t(16)=4.5$, $p<.001$, $d=2.23$, and crossed feet, $t(16)=5.8$, $p<.001$, $d=2.86$. The 6-month-olds only performed above chance with their feet in the uncrossed posture, $t(12)=6.7$, $p<.001$, $d=3.86$ (crossed: $t(28)=.4$, $p=.500$, $d=.24$). Significant comparisons are indicated (*= $p<.05$, **= $p<.01$, ***= $p<.001$).

Figure 1



Supplemental Information

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Supplemental data

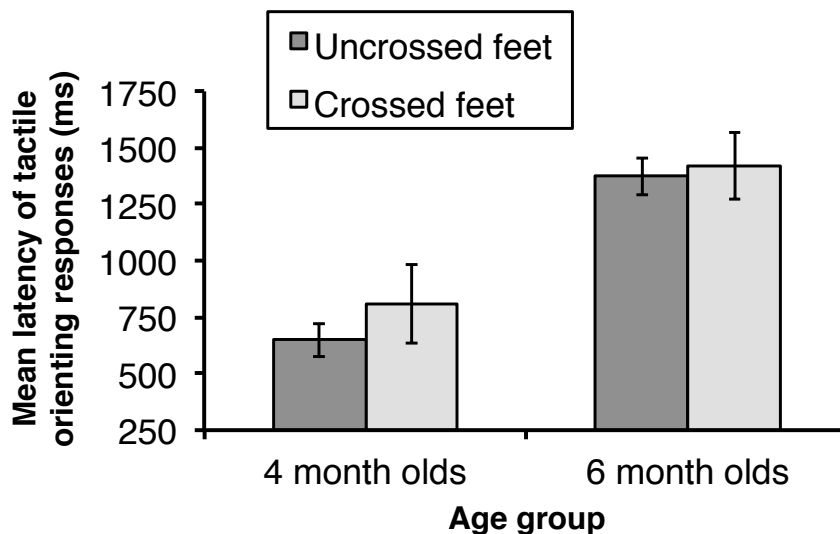


Figure S1 (related to Figure 1): Mean latency of the first unilateral foot movements to vibrotactile stimuli. Mean latencies were calculated from all of the infants' orienting responses (correct and incorrect) in which only a single foot was moved. Error bars indicate the standard error of the mean. The ANOVA revealed only a significant main effect of Age group, $F(1,28)=24.6$, $p<.001$, $\eta_p^2=.47$, in which the 4-month-olds ($M=729\text{ms}$, $SD=321$) responded more rapidly than the 6-month-olds ($M=1406\text{ms}$, $SD=612$). As described in the main text, this decline in response speed is consistent with an account of representational change in which more processing time is needed to locate a tactile stimulus on the body and in external space than on the body alone [9]. However, it is inconsistent with accounts appealing to increases in the efficiency of external spatial coding of touch with age. One such alternative interpretation of our findings is that the 4-month-olds were able to represent touch in external spatial coordinates, but that their equivalent performance across postures was due to having not yet developed prior expectations concerning the location of their feet in external space. Another related account explains the development of crossed-limb effects by appeals to increases in the automaticity of the external spatial coding of touch [S1]. However, far from predicting the significant increase in response latency between 4 and 6 months of age (across posture conditions) seen here, such accounts would rather predict decreases in response latency.

| <i>Posture condition</i> | | | | |
|---------------------------------|---------------------------|-----------------------|---------------------------|-----------------------|
| <i>Age group</i> | Uncrossed feet | | Crossed feet | |
| | <i>Mean no. of trials</i> | <i>Mean no. of</i> | <i>Mean no. of trials</i> | <i>Mean no. of</i> |
| | <i>completed (SD)</i> | <i>responses (SD)</i> | <i>completed (SD)</i> | <i>responses (SD)</i> |
| 4-month-olds (n = 17) | 12.41 (2.98) | 12.35 (2.94) | 12.24 (3.49) | 12.24 (3.49) |
| 6-month-olds (n = 13) | 12.69 (3.88) | 12.53 (3.82) | 12.46 (3.59) | 12.23 (3.46) |

Table S1 (related to Figure 1): Mean number of tactile trials completed and responded to across age groups and experimental conditions. On a proportion of the trials, the infants responded with both feet simultaneously. Given a greater difficulty in locating touches in the crossed as compared to the uncrossed posture (as seen in the 6-month-olds), we predicted that a greater proportion of simultaneous responses across both feet would be seen in the crossed-feet condition. Trends in numerical means confirmed this prediction, but due to the infrequent occurrence of dual foot responses, these trends were not statistically reliable. The mean proportion of responses which occurred in both feet for the 4-month-olds was .03 ($SD=.07$) in the uncrossed posture and .02 ($SD=.05$) in the crossed posture. The 6-month-olds' mean proportions of dual foot responses were .05 ($SD=.08$) in the uncrossed posture and .10 ($SD=.13$) in the crossed posture. Note here that the small numbers of dual foot responses made across the sample limit the power of any inferential analysis. However, the proportions were arcsine transformed and entered into a mixed 2 (Posture: Uncrossed / Crossed) x 2 (Age: 4-month-olds / 6-month-olds) ANOVA. The main effect of Age, $F(1,28)=4.0$, $p=.060$, $\eta_p^2=.13$, was marginally significant. No other main effects or interactions were found.

Supplemental experimental procedures

Design

Crossed limb deficits in tactile localisation have typically been observed in adults in the context of tactile temporal order judgments regarding pairs of stimuli presented in rapid succession to the hands [1]. However, the constraints of working with young human infants (who cannot respond to task instructions, and are not very willing to cross their hands) led us to record infants' orienting responses to a single tactile stimulus applied to the sole of one foot as a measure of tactile localisation, comparing the accuracy of responding across uncrossed and crossed feet posture conditions. Although recording visual orienting responses to tactile stimulation is possible with infants, previous [5] studies have found no reliable ability to localise tactile stimuli with visual fixation prior to 10 months of age. Here we recorded foot movements as a measure of orienting to tactile stimuli. Although crossed hands deficits in children's responses to tactile temporal order have not been observed prior to 5.5 years of age [S1], crossed hands deficits in manual responses to single tactile stimuli have been observed in infants [5], and crossed hands deficits in verbal reports of localisation to single tactile stimuli have been observed in the youngest age group tested so far with such a method [S2]. Crossed feet deficits in tactile localisation have been observed before in adults [1,S3].

Infants were presented with a maximum of thirty experimental trials. The 4-month-olds completed a mean of 24.9 trials ($SD = 6.2$), and the 6-month-olds completed a mean of 25.2 trials ($SD = 7.3$). Trials were presented in blocks of 10. In each experimental trial, a 1000ms vibrotactile stimulus was presented to one of the infant's feet, followed by an 8000ms response window. Every 5 trials, the posture of the infants' legs was changed from crossed to uncrossed or vice versa. Whether crossed or uncrossed posture was adopted at the start of each block was counterbalanced across participants. The same procedure was presented to both the 4- and 6-month-old infants.

Participants

Seventeen 4-month-olds (9 males), aged between 104 and 134 days ($M=116$ days; $SD=8$) took part in this study. Thirteen 6-month-olds (4 male), aged between 177 and 220 days ($M=196$ days; $SD=13$) also took part in the study. One additional female participant was tested but excluded from the analyses due to a failure of testing equipment. Informed consent was obtained from the infants' parents prior to commencing the study. The testing took place only if the infant was awake and in an alert and content state. Ethical approval was gained from the Ethics Committee of the Department of Psychology Goldsmiths, University of London.

Apparatus and materials

The infants were seated in a specialist baby chair. The seat was reclined in a horizontal position with the back-rest parallel to the floor. Adjustable straps secured the infant in the seat. Cotton padding and a head-rest were used to secure the posture of the infant's trunk. A digital video camera located 80 cm in front of the chair, facing the infant's frontal midline recorded the movements of the infant's feet. Video data were recorded for offline coding. The vibrotactile stimuli were delivered by two custom-built voice coil tactors (that the experimenter placed on the soles of the infant's feet, securing them in place with cohesive bandage) driven by a 220Hz sine wave and controlled by a custom E-Prime script. Additionally, signals were sent to a serial-controlled video titler to signal the onset and offset of the vibrotactile stimuli so that the infants' stimulus-locked behaviour could be observed and coded. Each tactile stimulus lasted for 1000ms, followed by 8000ms to allow sufficient time for the infant to react to the vibrotactile stimulus. Any noise emitted by the tactors was masked with grey noise played from a centrally placed loudspeaker. This masked sound cues for both the infant and experimenter.

Procedure

On each trial, the experimenter held onto the infant's legs and placed them in the assigned posture (uncrossed or crossed; approximately 10cm apart), whilst a second experimenter initiated the E-Prime program. At the start of each trial, the experimenter placed the infant's legs in the required posture. A trial was then triggered by the second experimenter. The first experimenter gently held the infant's legs in the assigned posture until the infant either moved their legs, or 8000 ms had elapsed, at which point the trial was terminated. In the 8000ms period following each stimulus, the experimenter oriented her face to the floor, in order not to distract the infant. If the infant became fussy, they were entertained with musical toys and/or bubbles until they were sufficiently settled to continue with the study. The study continued for as long as the infant was willing to co-operate, with participants completing a minimum of one block (10 trials), and maximum of three blocks (30 trials).

Data coding and analysis

The direction, latency, and type of infants' first foot responses to the tactile stimuli were coded from the video records. The initial 133ms after stimulus presentation were not coded as any movements occurring in this window were considered to be anticipatory. After this period, the first foot to move independently (of the other) was accepted as a unilateral foot response to the tactile stimulus.

Bilateral responses (i.e., the simultaneous movement of both feet) were recorded on a small proportion of trials, the details of which are described in the legend of Table S1.

When a unilateral response followed a bilateral response on any trial this was entered into the analyses of unilateral responses.

All recorded unilateral foot responses occurred within 6.7s and 7.03s of the tactile stimulus, for the 4- and 6-month-old infants respectively. 95% of foot responses occurred within 2.06s (4-month-olds) and 3.63s (6-month-olds).

All of the infants' unilateral foot responses were classified as either fine or gross withdrawal. Foot movements were identified as gross withdrawal if the leg and foot was pulled back towards the infant's truck. Fine movements included flexions and extensions of the knee, ankle, or toe joints. A second rater coded a proportion of the total trials across all participants for direction and latency with trial-by-trial agreement at 85%. Both raters were blind to the side of stimulus presentation, but were provided with stimulus onset and offset information. As described in the main text, we computed the proportion of total foot orienting responses that infants made with the foot receiving the tactile stimulus (i.e., correct unilateral responses / total number of responses). Raw proportion accuracy data and latency data are reported in the Figures and text. Analyses were performed on arcsin transformed accuracy data.

There were a total of 6 null responses across 751 trials over the whole sample (both age-groups), thus accounting for less than 1% of trials. This low rate of null response trials was seen across age groups (one such trial in the 4-month-old age group and five such trials in the 6-month-old age group across two participants). Independent sample t-tests confirmed that there was no difference in the proportion of null response trials across postures conditions in both the 4-month-olds, $t(16)=1.0$, $p=.33$, and the 6-month-olds, $t(12)=1.0$, $p=.34$.

In order to determine whether tactile orienting performance varied according to the stimulated foot (anatomically left vs. right foot), we conducted a mixed measures ANOVA of the proportion of accurate responses, including the factors of Stimulated foot (R / L), and Age (4-, and 6-month-olds). This revealed a significant main effect of Age group, $F(1, 28)=5.79$, $p=.023$, which is already described in the main manuscript. There was no effect of Stimulated foot, however, nor any interaction, indicating that there was no side bias in performance in either age group.

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